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STUDIES ON THE PRIMITIVE AXIAL SEGMENTATION OF THE CHICK.

BY JULIA B. PLATT.

WITH TWO PLATES.

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No. 4. — *Studies on the Primitive Axial Segmentation of the Chick.*[1]

By Julia B. Platt.

A. — The Succession of the Protovertebræ.

While studying the general development of the chick in connection with my special work upon the segmentation of the medulla and the origin of the cranial nerves, I came upon the following sentence in Balfour's Comparative Embryology: "The first somite arises close to the foremost extremity of the primitive streak, but the next is stated to arise in front of this, so that the first formed somite corresponds to the second permanent vertebra."[2] A foot-note calls attention to the fact, that "further investigations in confirmation of this widely accepted statement are very desirable."

Prof. His is hardly more definite. He says: "Die Urwirbel, welche zuerst entstehen, sind, wie dies v. Baer bereits richtig erkannt hat, nicht die vordersten Halswirbel, sondern es bilden sich vor den zuerst entstandenen Wirbeln im 5 und 6 Stadium noch einige fernere. . . . Ich möchte mit v. Baer vermuthen, dass ihrer jederseits zwei entstehen, möglicher Weise ist indess diese Schätzung zu niedrig gegriffen."[3]

I believe that the "Photogramme zur Ontogenie der Vögel, von C. Kupffer und B. Benecke," is the only other publication in which there is either confirmation or refutation of the opinion advanced by Balfour, in regard to the order in which the protovertebræ are formed. From the explanatory remarks with which Kupffer and Benecke accompany their beautiful photographs of chick embryos, one is led to think that the first protovertebra to appear is at least the fifth in the series, counting from the anterior. In determining the order in which the protovertebræ arise, they have been principally guided by the difference in size found to obtain among the protovertebræ of the same individual. The largest is considered the first.

[1] These studies were pursued in the "Annex" Laboratory at the Museum of Comparative Zoölogy, Cambridge, Mass., under the direction of Dr. Howard Ayers. Zoöl. Laboratory, No. 14.

[2] Vol. II. p. 161.

[3] Untersuchungen über die Erste Anlage des Wirbelthierleibes, pp. 82, 83.

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As my own investigations lead me to a conclusion at variance with that of Prof. Kupffer, I have examined the photographs with care, and am pleased to find that even in point of size the protovertebræ which I consider to appear first may well dispute the claims of Prof. Kupffer's first protovertebræ. In fact, the criterion of size among objects of such varying outline admits of a wide range of interpretation. It is not enough to judge from the superficial area, we must also take into account the depth. Moreover, it often happens that a large protovertebra appears opposite a small one, in which case size evidently does not determine seniority, since opposite protovertebræ are known to appear at about the same time. If precedence were established by size, then we should expect to find a gradual decrease in size from first to last; yet this is not what we do find, and Prof. Kupffer does not affirm that any protovertebra is second to be formed because second in size. Perhaps I am laying too much stress upon the matter of size, since what Prof. Kupffer says in this regard is quite conditional. He affirms only that, *if* size determines age, then we must consider this or that protovertebra first formed.

Moreover, it is not clear upon what Prof. Kupffer founds his opinion, that the second cleft in the mesoderm appears anterior to the first,[1] unless it be founded upon the relative distances of these two clefts from the anterior end of the primitive streak, as compared with the space which intervenes between the end of the primitive streak and the first mesodermic cleft in an embryo where only one cleft has yet appeared. This, at least, is the argument used in regard to Figure 25, *loc. cit.*, which represents a chick with four distinct pairs of protovertebræ, and a fifth faintly marked off in the mesoderm posterior to the others. Here the author considers the third from the anterior to be the one first developed, but allows that one might hesitate to decide between the third and fourth: "denn die Entfernung des hintersten Spalts von dem vorderen Ende des Primitivstreifs, harmonirt mit der Entfernung des ersten Spalts von demselben Punkte in den Figg. 20 und 22." (In Fig. 20 only one cleft has appeared in the mesoderm; in Fig. 22, there are but two.) "Mag man nun aber den einen oder anderen der beiden hinteren Urwirbel als den zuerst abgegliederten auffassen, jedenfalls geht aus den Figg. 24 und 25 hervor, dass die Segmentirung zunächst rascher nach vorn als nach hinten vorschreitet, und ist darnach die Angabe von Foster und Balfour zu berichtigen, die behaupteten dass die nächstfolgenden Urwirbel hinter dem ersten Paar entstünden."[2]

[1] Kupffer, p. 172.

[2] Ibid., pp. 173, 174.

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Now, Figures 20, 22, 25, are said to be enlargements of the anterior portion of Figures 19, 21, 24, respectively. In the last mentioned figures, the distance from the posterior extremity of the primitive streak to the head fold varies but little, while the primitive streak alone, in that chick which has three or four more protovertebræ than the other two chicks, is shorter by the width of those protovertebræ. Comparing the pictures, and allowing for a difference in total length, we find that the *width* of three protovertebræ has been added in Figure 24 from the region of the primitive streak to that of the embryo, and this added space we find occupied by protovertebræ. This being the case, does it not seem quite reasonable to suppose that the posterior vertebræ are developed later than the anterior, in the space once occupied by the receding primitive streak, — especially since we know the important part played by the primitive streak in the formation of the mesoderm? I do not attach much value to this argument, nor do I know if it would hold true for other chicks which might be photographed; I would merely say that these three photographs, which are compared by Prof. Kupffer for the purpose of determining the first protovertebra, are capable of leading to conclusions quite different from those at which the author arrives.

Prof. Kupffer further remarks: "An den Figg. 33 und 34 sind einige Einzelheiten hervorzuheben. Man geht wohl nicht fehl, wenn Man das in der Contourzeichnung mit *u'* markirte Urwirbel-paar [of five pairs, the fourth] als das erst entstandene auffasst. Abgesehen von der Grösse [it does not seem to me larger than either the second or fifth pair] spricht der Umstand dafür, dass die Axe der Urwirbel dieses Paares nicht senkrecht auf der Medianlinie steht, sondern eine leichte Neigung noch hinten zeigt. Es harmonirt das mit der Richtung der beiden ersten Spalten, Figg. 19–22."[1] Let me call attention to the fact, that the fifth pair of protovertebræ in Figures 33 and 34 shows also a "Neigung nach hinten," but is evidently not therefore considered "das erst entstandene."

I allow, indeed, that the obliquity of the angle made by the fourth and fifth pairs of protovertebræ with the main axis of the chick in Figures 33 and 34 corresponds well with the obliquity of the angle in Figures 19 and 22, where, as will be remembered, but one pair of protovertebræ is developed, and there is therefore no doubt about its being the first; but how in regard to Figure 23, where "der erste Urwirbel ist . . . deutlich begrenzt, vor demselben ein zweiter und hinter dem

[1] Kupffer, pp. 175, 176.

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ersten ein dritter in der Abgrenzung begriffen"?[1] Here the second pair of protovertebræ, the only pair as yet distinctly formed, is quite at right angles with the main axis of the chick, while the only one obliquely placed — the posterior — is not as yet fully formed, and therefore cannot be the first formed. Thus we see that, where there is but one pair of protovertebræ, it makes an oblique angle with the middle line; where there are three pairs, the third as yet but half defined protovertebra is oblique; and where there are five pairs, obliquity belongs to the last two pairs, of which the fifth is not as yet distinctly separated from the surrounding mesoderm. It seems, therefore, reasonable to suppose that the characteristic of obliquity to the middle line belongs rather to the protovertebra just formed, or forming, than to the protovertebra which of any given number was first formed.

Figure 41 represents a chick with seven pairs of protovertebræ, of which the fifth is marked as first. Figure 50 represents a chick with nine pairs, of which the fourth is designated first; and the author naively remarks, that "das Bild (Fig. 50) ist aufgenommen worden, um an einem zweiten Beispiele die Constanz der Erscheinungen an den Urwirbeln zu demonstriren." Four pairs of protovertebræ developed in front of the first in the less advanced chick; three pairs developed in front of the first in the more advanced chick. Shall we not call this variation, rather than constancy? I think enough has been said to show that neither the size of the protovertebræ, their relative distance from the primitive streak, nor yet their obliquity to the main axis, is a sufficient ground to warrant a decisive answer to the question in regard to the order of their development.

It may be that Prof. Kupffer has other reasons than those which he mentions for thinking it highly probable that the fourth or fifth pair of protovertebræ is the pair first developed; but in so far as the arguments he advances are concerned, one may well hesitate to accept his conclusions until they be supported by further evidence.

I have studied one hundred and fifty or more chicks, and from their external appearance I have been able to make out little in regard to the order in which the first protovertebræ are formed. The length of the chick at this early stage varies; the shape and relative length of the primitive streak vary; the outline of the area pellucida is seldom exactly the same in any two chicks. In fact, there seems to be no fixed point from which to measure. But I have been more fortunate in the study of serial sections. From these I learn that the cleft which sepa-

[1] Kupffer, p. 172.

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rates two protovertebræ is not at the time of its first appearance a continuous break extending throughout the width and depth of the vertebral plate. As a first trace of segmentation, there appears, in a line transverse to the axis of the chick, a succession of slight depressions on the dorsal surface of the vertebral plate. In a series of sagittal sections these depressions appear and disappear, a single depression seldom occupying more than two or three sections. As the chick grows, these depressions gradually deepen and become more continuous, while immediately below them a slight upward curve appears in the ventral boundary of the mesoderm. A little later, a distinct line appears, connecting these two indentations, and separating the cells of the undifferentiated mesoderm from those which are about to form a protovertebra. The latter now take on the spindle shape that characterizes the protovertebral cell, their long axes becoming gradually radial as regards the protovertebral body. Soon there appears here and there a break in the line that bounds the forming protovertebra, but, as a rule, cell prolongations, in a horizontal plane somewhat below the middle of the protovertebra, bind the new protovertebra, on the one hand to the undifferentiated mesoderm, and on the other to the protovertebra last formed.

The formation of a distinct and separate protovertebra takes place so gradually that a single long section shows the process in all stages of progression. Passing from the fully formed protovertebræ through four or five in process of formation, one reaches the undifferentiated mesoderm, in which a faint dorsal depression gives the first indication of the place where a protovertebra will ultimately be cut off.

This being the case, it is evident that, provided the order in which the protovertebræ are formed is in every chick the same, and provided that a protovertebra which has once started to develop continues to develop regularly, then, to determine the order in which they have developed requires but a sufficiently complete set of sectioned embryos.

In development, as in adult life, individual chicks may be expected, within a certain limited range, to vary from the typical chick. Still, if we find certain conditions to prevail in a large number of chicks, without exception, we are warranted in assuming these conditions to be normal. The protovertebræ are not formed until the mesoderm in the region of the somites has grown to be quite compact, and is as many as four cells deep, so that when the cell layers first take on their concentric arrangement they lie in two layers about the central axis of the protovertebra. I have never seen a protovertebra whose walls were

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but one cell thick, hence I am warranted in assuming that a certain thickness pertains to the mesoderm from which a protovertebra is immediately to be formed. Since the breaks in the mesoderm appear so gradually, it is possible, at the time the first cleft has appeared, to see where the next is to follow, and consequently to determine definitely on which side of the first protovertebra the first cleft appeared.

Figure 1, Plate I., is a section through a chick at the time when one decided parting of the mesoderm occurs, and the chick when examined entire by transmitted light showed but one mesodermic cleft.

From this section it will be seen that the first cleft lies anterior to the first protovertebra, not posterior, as Kupffer and Benecke supposed. A partial cut separates this protovertebra from the posterior mesoderm, while the protovertebra anterior to the first cleft is still closely connected with the mesodermic band which runs forward to the head. In fact, the anterior protovertebra is not entirely separated from the anterior mesoderm until as many as four or five protovertebræ have been formed. A curve in the dorsal outline of the mesoderm indicates from the first, however, where the anterior protovertebra is to be ultimately cut off. The series from which Figure 1 is taken shows more conclusively than any other series which I have, the relation of the first mesodermic cleft to the first protovertebra. It is difficult to find the exact stage when the first cleft is far more developed than the second, although the second one is already distinctly marked. However, in almost any series made at the time when the first protovertebra has just been formed, the same conclusion with regard to the priority of the anterior cleft may be reached by comparing the number of entire and partial breaks which occur in successive sections anterior to the first protovertebra with those that occur posterior to it. It will then be found that the anterior cleft is both deeper and more continuous than the posterior. The sections which I have drawn have been selected from chicks, the stages of whose development follow so closely upon one another, that, if it be supposed that between any two stages the protovertebra marked *a* has developed into that marked 1, while the cells included between the letters *f* and *g* have developed into the protovertebra *a*, then the protovertebræ, which in the preceding section were already partly cut off, posterior to 1, must have become attached to the mesoderm from which they were thus partly separated, or the order of development must vary in different chicks; for if the above supposition were true, in the chick with the greater number of protovertebræ the posterior ones would be less

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distinctly set off than in the chick with a less number of protovertebræ. The sections, however, do not support this supposition, since they show that, while the undifferentiated mesoderm posterior to the first protovertebra (1) is of the requisite thickness to permit of the formation of protovertebræ, the mesoderm anterior to *a* is too thin. This I find to be the case in all chicks which I have examined at this stage of development. Aside from the thinness of the mesoderm anterior to protovertebra *a*, the sections also show that even in the anterior part of *a* the cells have not increased as rapidly as in the posterior part. Consequently, this protovertebra is characterized by a peculiarly asymmetrical form, which gives it, in the early stages of its growth, an appearance quite different from that of the other protovertebræ. (See Figs. 2, 3, 4, and 6.)

Figures 5 and 5 a are taken from a series which was not cut parallel to the axis of the chick, and therefore the appearance of protovertebra *a* in Figure 5 is delusive. These facts force me to conclude that, contrary to the opinion advanced by Kupffer and Benecke, the development of protovertebræ is much more rapid caudad than cephalad. Indeed, after the first cleft in the mesoderm appears, dividing two forming protovertebræ, the posterior mesoderm goes on continually differentiating into protovertebræ until the chick acquires its complete number of protovertebræ, while it is only after three or four protovertebræ have been thus formed posterior to the first, that protovertebra *a* becomes finally separated from the anterior mesoderm, after which this mesoderm also slowly acquires sufficient thickness to form another protovertebra anterior to *a*.

Figure 5 a was drawn for the purpose of showing a group of cells lying between *f* and *g*. They come into section near the outer (i. e. lateral) boundary of the line of protovertebræ, and extend through only three sections, while it takes twenty sections to pass through a protovertebra. They are, in fact, the first indication of the formation of a protovertebra anterior to *a*. A like group of cells is not found on the opposite side, nor do they occur on either side of the chick from which Figure 6 is taken. But I find a similar group of cells in the same position (between *f* and *g*) in the series from which Figure 7 is drawn. The section represented is that which shows best the characteristic radial arrangement of these cells. Here, too, but few sections pass through the group. In the succeeding stages they are more marked, and by the time five or six protovertebræ have been formed posterior to 1, these cells have become distinctly *protovertebral* in their arrangement.

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Still the new protovertebra is little more than a half-protovertebra, for it is much smaller than those immediately behind, and opens anteriorly to the mesoderm of the head, into which it passes with no distinct boundary. These peculiarities of protovertebra *b* are evident even in the entire chick, if examined at this stage.

For some time I thought it possible that this incomplete protovertebra might be formed from protovertebra *a*, but this cannot be the case, for I have traced its growth from a few cells grouped together anterior to *a*, up to the time when the ninth nerve, passing behind the ear capsule, crosses so near to this protovertebra as to leave no intervening tissue from which another protovertebra could be formed. That another protovertebra is not formed anterior to *b* is also evinced by the fact, that in no subsequent stage does the line of protovertebræ end anteriorly in a *complete* protovertebra, or in a protovertebra *less complete* than *b*. If *b* became complete, and the tissue anterior to *b* developed into an incomplete protovertebra, it would be possible to find the stage in which this change took place.

In Kölliker's "Entwicklungsgeschichte des Menschen und der höheren Thiere," there is a figure[1] representing an "Urwirbel ähnlicher Körper *vor* der Gehörgrube, der von einem Ganglion und zwei Nerven gebildet wird." Another figure[2] represents an embryo with two large cell masses at the beginning of the protovertebral line, which Kölliker calls "Urwirbeln ähnliche Massen." He supposes them to represent the "vereinigte Anlage der Ganglion des Glossopharyngeus und Vagus." The shape of these last mentioned protovertebra-like structures, and their relative distance from the ear capsule, lead me to think it highly probable that their posterior wall is formed by the incomplete protovertebra (*b*) of which I speak above, while their anterior wall is formed by the ninth nerve. However this may be, since Kölliker affirms these structures to be at least in part *ectodermic*, they offer no objection to the limitation which I place upon the *mesodermic* protovertebræ, of which alone I speak.

My conclusions are, therefore, that the first break in the mesoderm occurs anterior to the first protovertebra, and that two protovertebræ (or, more correctly, one and a half) are slowly formed anterior to the first mesodermic cleft, in the time occupied by the formation of six or seven protovertebræ posterior to that cleft. With regard to the number of protovertebræ occurring anterior to the first, my work confirms the estimate of His and Von Baer.

[1] *Loc. cit.*, p. 430. [2] *Loc. cit.*, pp. 142, 143.

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In respect to the further development of these protovertebræ, I quote from Froriep,[1] the results of whose investigations have been corroborated by Van Wijhe. "In der Occipital region, *d. h.* in dem zwischen ersten Cervical-nerven und Vagus eingeschlossenen Abschnitt der Wirbelsäule, finden sich bei viertägigen Hühnerembryonen vier Muskelplalten, welche von hinten nach vorn (cranialwärts) an Grösse abnehmen. Es waren also hier vier Urwerbel angelegt, welche in den Aufbau des Kopfes eingehen. Der fünfte liegt auf der Grenze von Kopf und Halswirbelsäule, die Muskelplatte, die dieser liefert, berührt mit ihrem caudalen Rand die Anlage des ersten Halswirbelbogens, mit dem cranialen die hinterste Bogenanlage der Occipitalgegend."

We see, therefore, that the first mesodermic cleft divides evenly the four pairs of protovertebræ which enter into the formation of the head, and that this cleft does not coincide with the occipito-cervical cleft of the adult.

B. — The Relation of the Cranial and the Spinal Nerves to the Neural Axis.

The development of the rudimentary protovertebra *b* brings me to that stage in the growth of the chick with which my work ostensibly began. Contemporaneously with the formation of this protovertebra, the successive constrictions of the medulla appear, the neural crest is formed, and the first cranial nerves arise (V., VII., VIII.).

If a chick be examined by transmitted light during the second or third days of incubation, it will be noticed that the medulla is marked by a series of swellings and constrictions which are directly continuous with a line of similar swellings and constrictions in the region of the spinal cord. These divisions of the medulla are such noticeable characteristics that they have frequently been mentioned before the comparatively recent attempts to determine the number of head-segments from the distribution of the cranial nerves. His, Rabl, and Balfour speak of them as more or less transitory structures; but in so far as I know, Béraneck and Orr are the only authors who have attempted to elucidate by their means the problem of cranial segmentation.

In an article upon the cranial nerves of the Lizard,[2] Béraneck describes five successive enlargements of the central canal of the

[1] Archiv Anatomie und Physiologie, 1883. Zur Entwickelungsgeschichte der Wirbelsäule, p. 226.

[2] Des Nerfs Crâniens chez les Lézards. Recueil zoologique Suisse, 1884.

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medulla, corresponding to which the external surface of the neural wall is marked by five encircling swellings. These he designates "replis médullaires," (designated by Dr. Orr "neuromeres,") and he attempts to assign to them a segmental value, from their constant relation to certain of the cranial nerves. With the anterior neuromere he finds the fifth nerve connected; with the third, the united seventh and eighth nerves, while the roots of the ninth nerve come from the fifth neuromere.

Dr. Orr, in a recent publication upon the development of the Lizard,[1] gives a similar description of the relation existing between the neuromeres (replis médullaires) and the fifth, seventh, and ninth cranial nerves. Béraneck has also published a detailed account of the neuromeres in the chick,[2] and has assigned to each fold a segmental value. The two anterior folds correspond to the two head-segments supplied by the fifth nerve. The third neuromere belongs to the united seventh and eighth nerves, these nerves consequently representing but one primitive segmental nerve. The fourth neuromere he assigns to the segment of the auditory capsule and sixth nerve, believing the relation which obtains between the auditory capsule and eighth nerve quite secondary. The fifth neuromere is connected with the ninth nerve. The tenth nerve represents a transitory condition between a spinal and cranial nerve, and is consequently not entitled to its neuromere, since the swellings and constrictions in the region of the spinal cord are not considered by Béraneck structures homologous with the neuromeres.

Béraneck claims to have found similar folds in tritons and elasmobranchs, although he was deterred from establishing their relation to the cranial nerves by lack of material. To the above list of vertebrates possessing neuromeres, I can add the salmon. Between the ages of fourteen and nineteen days the medulla of the salmon is divided into five distinct lobes or neuromeres, with the anterior of which the fifth nerve is connected; with the third, the ganglion of the seventh and eighth nerves, while the ninth nerve passes from behind the ear capsule close to the fifth neuromere. I did not have sufficient material, at the age when the nerves first appear, to decide whether this relation between nerves and neuromeres is primitive or secondary. From the constancy with which *five* neuromeres appear in classes so widely separated as fish, reptile, and bird, they would seem to be structures inherited from a common ancestral form. Moreover, the constancy in the number of

[1] Embryology of the Lizard. Journal of Morphology, 1887.

[2] Replis Médullaires du Poulet. Recueil zoologique Suisse, 1887.

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neuromeres is not less striking than the constant relation which the first, third, and fifth neuromeres bear to the fifth, seventh, and ninth cranial nerves.

The constrictions which in the chick divide the neural tract into cerebral vesicles or "neuromeres," appear even before the neural walls have formed a closed canal. They arise successively from before backwards, dividing the medullary tube into vesicles, which decrease in size in the order of their formation. The third neuromere of the medulla (fifth vesicle formed) is the only exception to the gradual diminution of the successive vesicles. This neuromere (Fig. 17, Plate II.) is smaller than either the second or fourth.

Anterior to the first protovertebra the neural canal is divided by a series of such constrictions into seven vesicles. With the appearance of each successive protovertebra, another constriction occurs opposite the protovertebra, and another neuromere (as we may also designate these neural swellings) is added to the preceding. The constrictions of the spinal cord often appear before the formation of the corresponding protovertebræ; consequently these ectodermic differentiations are quite independent of any mechanical influences consequent upon the formation of the protovertebræ.

Béraneck has already carefully described and figured the medullary folds, and in as far as the folds themselves are concerned I can but confirm the results of his investigations; yet I have ventured to repeat the description in brief, because I would call attention to the fact, that in the chick, at least, the order in which the various parts of the brain are formed does not correspond with what is usually given as the typical development of the vertebrate brain.

Wiedersheim says: "At a very early stage three swellings may be seen on the anterior enlarged part of the medullary tube, which are spoken of as the primary anterior, middle, and posterior cerebral vesicles (fore-, mid-, and hind-brain). . . . The primary fore-brain and hind-brain each become differentiated into two parts, and thus five divisions of the brain may be distinguished. Counted from before backwards, these are Prosencephalon (secondary fore-brain), Thalamencephalon (primary fore-brain), Mesencephalon (mid-brain), Metencephalon (secondary hind-brain), and Myelencephalon (primary hind-brain)."[1] I quote from Wiedersheim, because he expresses so concisely the opinion commonly advanced by zoölogists in regard to the formation of the vertebrate brain.

[1] Comparative Anatomy of Vertebrates, pp. 181, 182.

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From Figure 17, Plate II., it will be seen that the primitive brain of the chick does not correspond with the above description. As the result of my studies, I find that primarily the chick's brain consists of a succession of neural vesicles, from the first of which the three anterior divisions of the adult brain are developed, namely, Prosencephalon, Thalamencephalon, and Mesencephalon. Soon after the formation of the first cerebral vesicle, the optic lobes appear as lateral outgrowths from it, after which, for some time, the growth of this vesicle is not relatively greater than the growth of the following vesicles, or than that of the entire embryo. But with the first appearance of the cranial flexure, the primary fore-brain begins to develop very rapidly, soon a constriction marks off the mid-brain (Fig. 15), after which the fore-brain grows out as an anterior vesicle, so that by the time the head is completely bent, the primary fore-brain is represented by three large vesicles, which open widely into each other (Fig. 14). The development of these three vesicles is wonderfully rapid, and since it is exactly coincident with the cranial flexure one may well connect the two events causally, affirming the cranial flexure to result from the very rapid development (increase of surface) of the dorsal and lateral walls of the first cerebral vesicle.

The second primary vesicle develops into the cerebellum, and the successive vesicles, including the neural swellings between the first five protovertebræ, take part in the formation of the adult medulla oblongata. Thus, either the development of the brain in the chick forms a marked exception to the usual development of the vertebrate brain, or the nomenclature of the three primary cerebral vesicles is inaccurate. The prevalent impression, that the brain consists primarily of but three vesicles, may possibly arise from the fact that the ectoderm does not exactly follow the neural conformation. The surface of the head at an early stage presents three main divisions, marked by slight constrictions, but these are quite independent of the neural tract. The difference between the contour of the head and that of the brain will be manifest if the chick be first examined as an opaque object, and then by transmitted light. In the former case, the superficial outlines of the head are most apparent; in the latter, the medullary walls come into strong relief.

Although I agree with Orr and Béraneck in regard to the number and appearance of the neuromeres, and although I also find the ultimate relation of the cranial nerves to these folds in salmon and chick to be the same as that which they describe for lizard and chick, I do *not*

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find that this relation is a primitive one in the chick. From lack of material, I was unable to study the younger stages of development in the salmon; but with regard to the chick, I can say definitely that at its first appearance the fifth nerve does *not* arise from the outward convexity of the first neuromere of the medulla, as Béraneck has represented it. It arises from the concavity that lies between the first and second neuromeres, and its position at the side of the anterior neuromere is quite secondary. This fact supports Marshall's theory, that segmental nerves "at an early period shift downwards, and acquire new or secondary roots of attachment to the side of the brain."[1] It has seemed to me that the secondary attachment of the fifth nerve was not due to a new outgrowth connecting the nerve root and brain, but rather to a gradual shifting of the position of the original root. However this may be, it certainly cannot be owing to the outward spreading of the walls of the fourth ventricle that the root of the fifth nerve comes to acquire an attachment anterior to its primitive attachment. Béraneck says: "Par suite des changements survenus dans la roûte du cerveau postérieur, . . . les replis sont encore plus déjetés sur les côtés de la région céphalique et les racines nerveuses paraissent être descendues et se rattacher plus près de la région ventrale qu'auparavant. . . . Les changements survenus dans la forme et la structure du cerveau postérieur me semblent suffire à expliquer cette descente apparente des nerfs crâniens sans qu'il faille recourir à une hypothèse ne reposant sur aucune observation directe."[2] The mere divergence of the walls of the fourth ventricle may suffice to explain the more ventral attachment of the fifth nerve, but is hardly sufficient to account for the fact that its secondary attachment is anterior to the first.

Since the walls of the fourth ventricle follow quite closely the curves on the outward surface of the medulla, the concavity from which the fifth nerve arises is represented on the inside by a ridge projecting far into the fourth ventricle. A series of horizontal sections through the root of the fifth nerve at the time of its attachment between the first and second neuromeres shows this ridge to be composed of lines of cells converging like the rays of a fan towards the point from which the fifth nerve takes its origin (Fig. 10). This convergent arrangement of lines of cells is characteristic of each of the ridges which, projecting into the fourth ventricle, separate successive neuromeres (Fig. 12 b). If

[1] A. Milnes Marshall. Segmental Value of the Cranial Nerves. Journal of Anatomy and Physiology, 1882.

[2] Replis Médullaires du Poulet, Rec. zool. Suisse, pp. 334, 335.

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Figure 10 be examined, it will be seen that the fifth nerve draws its fibres from both the posterior part of the first neuromere and the anterior part of the second. Succeeding sections show the connection between the nerve and the neuromeres, both anteriorly and posteriorly, to be more extensive than in the section drawn. Béraneck says, apropos of the connection between the fifth nerve and second neuromere: "J'avais toujours été frappé de ce que la seconde paire des replis médullaires était la seule ne paraissant avoir aucune relation avec les nerfs crâniens. En étudiant la question d'un peu plus près je reconnus que cette deuxième paire émet un tronc nerveux qui vient se fondre avec celui partant de la première. Ainsi les éléments qui constituent le trijumeau sont fournis par les deux premières paires des replis médullaires. . . . Le trijumeau correspondant à deux paires de replis, ne serait donc pas un nerf simple, mais résulterait de la fusion de deux troncs nervaux primitivement indépendants." [1]

From the fact that the second neuromere, as well as the first, contributes fibres to the formation of the fifth nerve, I cannot argue, as Béraneck does, that these two neuromeres correspond to the two primitive segments to which, from its peripheral distribution, the fifth nerve is supposed to be related.

Of the two segmental nerves united in the fifth, one is surely represented by the main branch of the fifth with its Gasserian ganglion, the other segmental nerve is usually supposed to be represented, at least in part, by the ramus ophthalmicus profundus, with its ciliary ganglion. In fact, Van Wijhe claims to have traced in the elasmobranch the backward growth of the ramus ophthalmicus, from its connection with the brain in the immediate neighborhood of the ciliary ganglion to its final fusion with the main body of the fifth nerve. This being the case, one would hardly look for the neuromere of that anterior segmental nerve, which has thus lost its independence, back of the neuromere to which the fifth nerve is itself attached. It is possible, indeed, to suppose that the whole fifth nerve has transferred its connection from the posterior to the anterior neuromere, but such a supposition takes away any segmental value which may attach to the neuromeres from their present relation to the cranial nerves.

Aside from any theory of segmentation, the fact remains that the fifth nerve, at the time of its origin, arises from the depression between the first and second neuromeres, while the cells composing its root are intimately connected with the cells forming the mass of the ridge which

[1] *Loc. cit.*, p. 337.

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projects into the fourth ventricle, opposite the external attachment of the nerve. It is therefore with this inner swelling, and not with an outer one, that the fifth nerve is originally connected. It may here be noticed, that neither the third nor fourth cranial nerve arises from the middle of the vesicle with which it is connected, but both are attached to the brain near the line which separates this vesicle from the following.

Passing from the concavity between the first and second neuromeres to that which separates the second and third, or, in other words, passing from the first medullary ridge (using this term to designate the internal ridges) to the second, we come to the origin of the seventh nerve, anterior to the small neuromere beside which lies the ganglion of the united seventh and eighth nerves. In a series of horizontal sections made at the time when these nerves have just left the neural crest, it will be found that from each side of the third neuromere nerve fibres pass downward and towards the middle of that neuromere, where they unite in a large ganglion. (See Fig. 12 b.) This ganglion is ultimately and secondarily connected with the convexity of the third neuromere. As I remarked above, this neuromere is smaller than any other anterior to the origin of the tenth nerve, consequently the space included between the large roots of the seventh and eighth nerves is small, and might easily be overlooked in transverse or sagittal sections. (See Fig. 12 a.) The long axes of the cells composing each nerve are, as usual, parallel to each other, but since the two nerves meet the ganglion from different directions, it follows that the long axes of the cells composing the seventh nerve make an angle with the long axes of those composing the eighth nerve, and the ganglion is consequently connected with the brain by two bands of cells whose long axes diverge (Fig. 12 a.)

Although the fibres of the ninth nerve lie in close proximity to the fifth neuromere, they may be traced back of the ear capsule to the concavity which separates the fourth and fifth neuromeres, and corresponds to the fourth medullary ridge. (See Figs. 11 and 11 a.) The first figure shows the course of the nerve, and passes through the neural crest. The second figure is drawn to show the relation of the nerve to the entire ear capsule and the medullary ridge. They are from the same series.

Posterior to the ninth nerve, the long commissure of the tenth nerve extends beyond the fourth protovertebra. The peripheral distribution of this nerve, and the extent of its commissure, show it to be composed of the fused roots of several spinal nerves. All of the spinal nerves arise opposite the muscle plates (Figs. 13, 13 a) from correspond-

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ing concavities in the spinal cord. The nerve fibres primarily connecting the spinal ganglia with the cord, form an almost continuous sheet extending along each side of the spinal cord. At intervals corresponding to the interspaces between the protovertebræ, these fibres are apparently pushed to either side by the thickened mesoderm which projects upward from the region of the notochord, so that the fibres between every two such mesodermic thickenings are drawn into one spinal ganglion. The width, therefore, of the band of fibres connecting a spinal ganglion with the spinal cord, corresponds to the width of the protovertebra lateral to it (Figs. 13, 13 a). From a glance at the general relation of the neural concavities to the nerves which arise from them, it will be noticed that, where the ganglion is connected with the neural axis by a mass of fibres bound closely together, the curve of the concavity from which they arise is sharp, as in the region of the medulla. Where the fibres are spread out, forming a wide ganglionic connection, the curve of the concavity is gentle, as in the spinal cord. But whether its curve be gentle or sharp, the concavity in both medulla and spinal cord is the source from which the nerves originate, and the neural swellings which correspond to the nerve roots are the inner ridges, not the outer neuromeres.

Béraneck is unwilling to homologize the neuromeres of the medulla with the swellings of the spinal cord, because of the difference in the later differentiation of the nervous tissue in these two regions, and because, as he affirms, the swellings of the spinal cord are transient. But so are also the neuromeres of the medulla. By the fifth day of incubation they are fast fading away, yet at this time the wave-like form of the walls of the spinal cord is still plainly visible (Fig. 13). Here, as in the medulla, the segmentation is more manifest in the ventral region than in the dorsal. Moreover, at the time when the neuromeres of the medulla and the swellings of the spinal cord first appear, the tissue throughout the neural tract is quite indifferent. Further, since the first four folds posterior to Béraneck's *five* medullary folds lie also in the region of the medulla, and are also connected with a cranial nerve, — viz. the tenth, — it is practically impossible to draw the line separating these folds from the more anterior. It is true that they are smaller, but the difference between the fifth neuromere and the next posterior fold is not as great as the difference between the second and third neuromeres. I therefore see no reason why the successive swellings which originally mark the neural tract should not be regarded as homologous structures.

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Orr says: "Balfour described certain internal swellings of the lateral wall of the hind-brain of elasmobranch embryos: 'Swellings of the brain towards the interior of the fourth ventricle are in connection with the first five roots of the vagus and the glosso-pharyngeal root, and a swelling is also intercalated between the first root of vagus and the glosso-pharyngeal root.' In his figure (Fig. 5, Pl. XVI., *l. c.*) there are no external marks of these divisions, and the 'swellings' lie opposite the nerve roots while in the region between the nerve roots there are internal depressions. In the lizard, on the contrary, in the region between the nerve roots are internal ridges. The two conditions are thus very different; but possibly younger elasmobranch embryos might show a connection between these swellings and neuromeres."[1] My experience with the chick leads me to believe that possibly younger stages in the development of the lizard than those which either Orr or Béraneck was able to study may show a connection between the "swellings" and the nerve roots.

[1] *Loc. cit.*, pp. 336, 337.

JULY, 1889.

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EXPLANATION OF THE PLATES.

LETTERING.

d, first cleft in the mesoderm.
o, *i*, *j*, *k*, *l*, indicate respectively successive clefts in the mesoderm posterior to the first cleft, *d*.
f, *g*, position of first and second clefts anterior to *d*.
1–6, successive protovertebræ posterior to the first mesodermic cleft, *d*.
a, *b*, first and second protovertebræ anterior to the first cleft, *d*.
III., V., VII., VIII., IX., X., third, fifth, seventh, &c. cranial nerves.

A. Prosencephalon.
B. Thalamencephalon.
C. Mesencephalon.
D. Metencephalon.
E. Myelencephalon.
aud. auditory capsule.
ect. ectoderm.
h. heart.
inf. infundibulum.
m. p. muscle plate.
n. c. neural crest.
n. ch. notochord.
n. sp. spinal "neuromeres."
p. v. protovertebræ.
sp. g. spinal ganglion.
v. fourth ventricle.
x. section broken.

1′, 2′, 3′, 4′, 5′, neuromeres of the medulla.

PLATE I.

Sagittal sections, showing the development of the protovertebræ.

Fig. 1. The first mesodermic cleft is seen anterior to the first protovertebræ. × 60.
Fig. 1 a. Same, enlarged. × 180.
Fig. 2. Section from an embryo with two protovertebræ, showing the peculiar shape of protovertebra *a*, which is due to the less rapid proliferation of cells in its anterior portion. × 330.

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Fig. 3. Embryo with three protovertebræ. The shape of protovertebra *a* much the same as in the embryo of two protovertebræ. × 330.

Fig. 4. Section from a chick with four protovertebræ. × 180.

Fig. 5. " " " five " × 160.

Fig. 5 a. " " " five " × 160.

Fig. 6. " " " six " × 160.

Fig. 7. " " " seven " × 165.

Between *f* and *g* is seen the beginning of the protovertebra anterior to *a*.

Fig. 8. Sections from a chick with eight protovertebræ.

PLATE II.

Fig. 10. Horizontal section showing the origin of the V., VII., and VIII. cranial nerves in a chick with fifteen protovertebræ.

Figs. 11, 11 a. Two sections from the same series. Fig. 11 shows the origin of the IX. nerve from the neural crest back of the auditory capsule (*aud.*). Fig. 11 a is a more ventral section, showing the relation of the ear capsule to the neural concavity dorsal to which the IX. nerve arises. Horizontal sections.

Fig. 12. Shows the neuromeres between which the nerves arise, as indicated. Sagittal section.

Fig. 12 a. Sagittal section, showing the two roots of the VII. and VIII. cranial nerves.

Fig. 12 b represents the right medullary wall from a horizontal section, showing the cell arrangement of the neural ridges connected with the VII. and VIII. cranial nerves.

Figs. 13, 13 a. Sections from two 4½-day chicks. They show the relation of the spinal ganglia (*sp. g.*) to the muscle plates (*m. p.*), and to the neuromeres of the spinal cord (*n. sp.*). 13 a is sagittal; 13, horizontal.

Fig. 14. Median sagittal section, showing the relation of the five main divisions (A, B, C, &c.) of the brain, after the cranial flexure.

Fig. 15. Median sagittal section, showing their relations at the beginning of the cranial flexure.

Fig. 16 shows the neural ridges in the medulla of a five-day chick. The roof of the fourth ventricle and mid-brain have been removed.

Fig. 17. Diagrammatic representation of the relation of the successive cranial vesicles at the time of their first appearance.

Fig. 18. Sagittal section through the lateral wall of the medulla in a five-day chick. In hardening, the mesoderm has broken away from the neural wall.

Fig. 19. Sagittal section near the middle line of the brain of a four-day chick.

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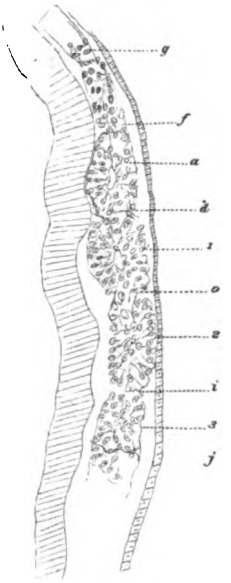
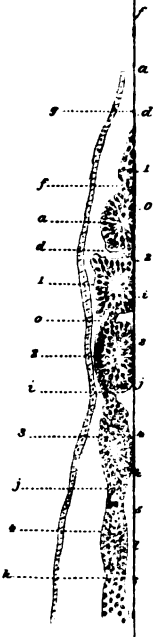
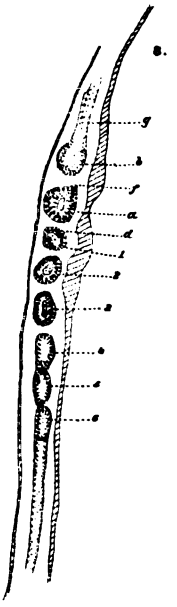
PLATT - CHICK.

PLATE. I.







B. Meisel. lith.

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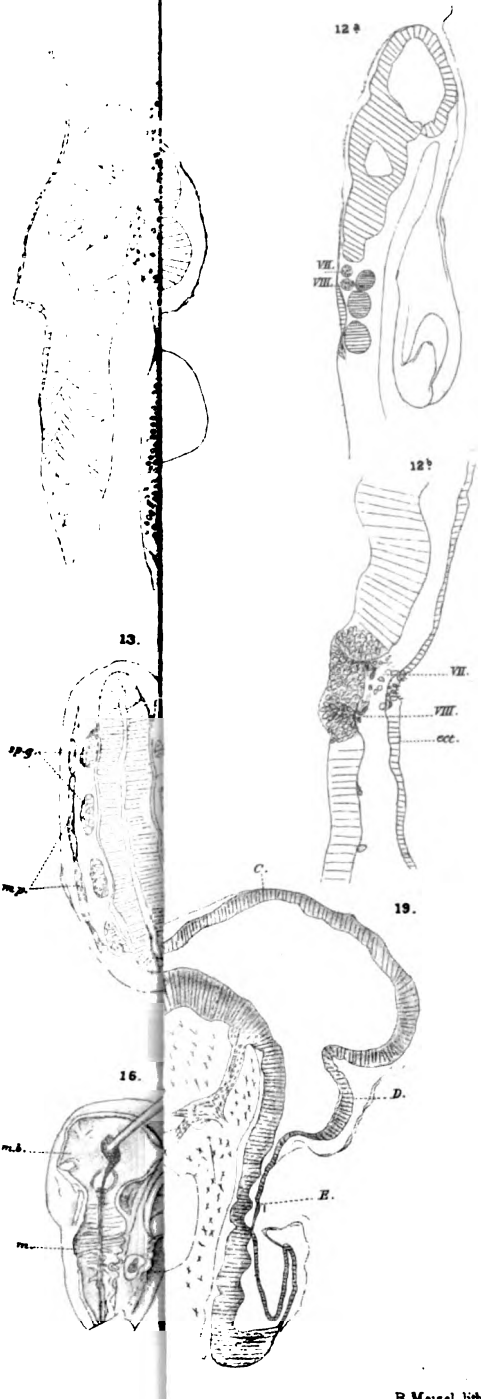

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